



TITLE:

Dental metric variability associated with human migration from skeletal remains of two Jomon sites (Yoshigo and Inariyama) in the Atsumi Peninsula area

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CITATION:

MORITA, WATARU ...[et al]. Dental metric variability associated with human migration from skeletal remains of two Jomon sites (Yoshigo and Inariyama) in the Atsumi Peninsula area. *Anthropological Science* 2012, 120(2): 167-177

ISSUE DATE:

2012

URL:

<http://hdl.handle.net/2433/161800>

RIGHT:

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1 Original Article

2 Article Title: Dental Metric Variability Associated with Human Migration from Skeletal Remains of Two

3 Jomon Sites (Yoshigo and Inariyama) in the Atsumi Peninsula Area

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Abstract

This study investigated inter-population genetic relationships in the Jomon Atsumi Peninsula area, comparing the pattern of human migration revealed by strontium isotope ratio with dental metric variation of Yoshigo and Inariyama skeletal remains. Morphological differences were evaluated between the local and immigrant groups to determine whether or not local populations had become completely homogenized by human migration. We made 4 x 4 contingency tables consisting of four clusters derived from *K*-means clustering of dental measurements and four groups (immigrants and locals of the two sites), and evaluated their correlations by Fisher's exact test. The results revealed that human migration pattern was significantly correlated with dental metric variation, suggesting that there was regional heterogeneity among Jomon populations in the Atsumi Peninsula area. Although the distinction between immigrants and locals of Yoshigo and Inariyama populations based on strontium isotope analysis was not completely in accord with dental metric variability, most of the identified immigrants exhibited dental profiles that were beyond each local profile as determined using Principal Component Analysis. Furthermore, the dental metric variances of the immigrants were significantly larger than those of the locals, suggesting their multiple origins. The microdifferentiation among populations in the Atsumi Peninsula area may suggest nonrandom kin-structured migration and/or population aggregation from surrounding areas.

Key words: dental metric, within-group variation, Jomon period, strontium isotope, migration

Introduction

The Jomon period spanned from 13000 to 2300 years BP in the Japanese Archipelago (Imamura, 1996a; Habu, 2004). The Jomon people were Neolithic hunter-gatherers who are well known for their cord-marked pottery. They generally led a sedentary life and effectively exploited marine and terrestrial resources. In the Late to Final Jomon period (ca. 4000–2300 years BP), the Jomon population declined due to the climatological cooling and associated environmental changes (Koyama, 1978), while they developed ritual practices and artifacts without drastic changes in subsistence strategies (Imamura, 1996a; Habu, 2004). Then, the Jomon culture eventually ended with waves of migration of agriculturalists with wet rice cropping from continental East Asia, except for Hokkaido (Imamura, 1996b; Chisholm and Koike, 1999; Tsude, 2001; Kobayashi et al., 2004).

The Atsumi Peninsula area (the Atsumi Peninsula and its surrounding area of the Tokai region in a central part of the Japanese Archipelago) is one of the areas where many Jomon shell mounds are situated. In this region, the number of shell mounds began to increase from the beginning of the Late Jomon period (ca. 4000–3000 years BP), and many of them were formed during the Final Jomon period (ca. 3000–2300 years BP). Despite the general population decline through the Late to Final Jomon period, the Tokai region still retained a greater population density than the eastern Chubu and Kanto regions, and western Japan (Koyama and Sugito, 1984).

Shell mounds in the Atsumi Peninsula area are characterized by an extremely large number of human burials. Most of these skeletons were excavated in the 1920's and became important materials for the early study of the origins of the modern Japanese (Kiyono, 1925, 1928). It is also notable that these sites revealed interesting ritual and burial customs such as tooth ablation practices, tooth filing, and squared-shaped bone-pile burial (banjo-shuseki-bo), spurring many archaeological studies on the social organization and mortuary habits of the Jomon people (Harunari, 1979, 1986; Tanaka, 2001; Funahashi, 2008). Jomon people from the Final period especially around eastern Japan are thought to have had a transegalitarian

society in which socioeconomic inequalities were recognized (Hayden, 1995; Takahashi, 2004). Watanabe (1990) proposed that occupational differentiation had appeared in the Jomon society, on the basis of an ethnographic comparison with recent sedentary hunter-gatherers. The presence of interfamilial occupational differentiation (hunting vs. fishing) of the Jomon people in the Atsumi Peninsula has been supported by carbon, nitrogen and strontium isotope analyses (Kusaka et al., 2008, 2011), suggesting an increased social complexity in the Final Jomon period.

Hints for reconstructing past social structures can also be obtained from biodistance analysis, which employs phenotypic data as proxies for underlying genotypic variation to define relatedness or divergence between populations (Larsen, 1997, 2002). Inter-population phenotypic variation is formed through genetic drift (human settlement, population growth/decline) and gene flow (human migration) (Lane and Sublett, 1972; Spence, 1974; Konigsberg and Buikstra, 1995; Stojanowski and Schillaci, 2006). Matsumura's (2000) dental metric study on skeletal remains from four sites in the Atsumi Peninsula area (Yoshigo, Inariyama, Ikawazu and Hobi Shell Mounds) revealed that most of the individuals from these four sites did not form clear site-specific clusters, although some individuals from a given site formed tight clusters, which might have reflected close kinship. This result raises two different possibilities. The first one is that genetically homogeneous populations had been dispersed in this area before the Late Jomon period. The second one is that local gene pools had not been totally homogenized but mutual human migration masked morphological distinction between populations.

Analysis of phenotypic variation alone cannot decide which was the case. Kusaka et al. (2009, 2011) made distinctions between "locals" and "immigrants" in subsamples of the Yoshigo and Inariyama populations by strontium isotope analysis of the tooth enamel. Strontium isotope analysis is an effective tool to reveal prehistoric human migration patterns (e.g., Ezzo et al., 1997; Price et al., 2002; Bentley et al., 2007; Knudson and Price, 2007; Montgomery et al., 2007). Tooth enamel records the Sr isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) in the environment where the person lived during the formative period of the tooth enamel and undergoes little

subsequent change. Therefore, when people migrate between geochemically contrasting residential areas, the Sr isotope signatures in the tooth enamel of immigrants are detectable (Bentley, 2006). In the Atsumi Peninsula area, strontium isotope ratio has small variation in each local area around the site, and large differences of regional strontium isotope ratio exist (Kusaka et al., 2009, 2011). Since the observed strontium isotope ratio in tooth enamel are sufficiently contrasted between locals and immigrants, immigrants of populations in the Atsumi Peninsula area can be successfully identified. Although the “local group” determined by strontium isotope ratio may include immigrants who came from a place with the same geochemical signature as the excavated site, these determinations help us to evaluate morphological similarity/dissimilarity between the local group and immigrants. Genetic variability among populations is affected by local demographic variables, especially by human migration patterns and frequencies. Recently, biodistance studies have been employed to reveal intra-site genetic variation (Buikstra et al., 1990; Stojanowski and Schillaci, 2006). There are several applications for Jomon populations (Kondo, 1994; Matsumura et al., 1996; Matsumura and Nishimoto, 1996) and some has been done being cross-checked with ancient DNA data (Shinoda et al., 1998; Adachi et al., 2003, 2006). Although the exact nature of genealogical relationships among individuals can be rarely specified without *a priori* knowledge, biodistance analysis can reveal relative relatedness among them (Stojanowski and Schillaci, 2006). If morphological distinction is not observed between the local and immigrant groups, a whole population in an area was in fact genetically homogeneous. On the other hand, if any morphological distinction is found, human migration between populations had not completely homogenized local gene pools.

The purpose of the present study is to reveal inter-population genetic relationships in the Atsumi Peninsula area, by comparing dental metric variation to human migration based on strontium isotope analysis of Yoshigo and Inariyama Jomon skeletal remains. This study represents a synthesis of biological relationships within and between populations and archaeological contexts to reconstruct the biocultural structure in the Atsumi Peninsula area, using information uniquely available from strontium isotope

118 analysis.

119

120 **Materials and Methods**

121 The materials examined in this study consisted of human skeletal remains from Yoshigo and Inariyama
122 Shell Mounds in the Atsumi Peninsula area (Figure 1; Table 1). These skeletal series were housed in the
123 Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University. The Yoshigo Shell
124 Mound is located on the northern coast of the Atsumi Peninsula, Aichi Prefecture. In 1922, K. Kiyono
125 excavated this site and recovered about 300 human skeletons (Kiyono, 1969). The formation of the Yoshigo
126 site covers the later part of the Late Jomon period and the Final Jomon period (ca. 3500–2300 BP), based on
127 the chronology of pottery types (Yamanouchi, 1952). This chronology was confirmed by radiocarbon dating
128 of human bone collagen (ca. 3200–2800 cal BP; Kusaka et al., 2009). The Inariyama Shell Mound is
129 located on the Toyohashi Plain, Aichi Prefecture. This site was also excavated in 1922, and about 60 human
130 skeletons were recovered (Kiyono, 1969). The age of Inariyama is thought to be the middle and late part of
131 the Final Jomon period (ca. 2800–2300 BP) based on the chronology of pottery types. The radiocarbon
132 dates of remains from Inariyama Shell Mound have not been investigated. Age and sex, and the distinction
133 between immigrant and local skeletal remains as well as cut-off values of local strontium isotope ratios are
134 given in Kusaka et al. (2009, 2011). Figure 2 illustrates the strontium isotope ratios of tooth enamel of
135 Yoshigo and Inariyama skeletal remains with distinction between local and immigrant. Eight out of 24
136 individuals of Yoshigo and three out of ten individuals of Inariyama were identified as immigrants (Figure
137 2).

138 Dental crown metrics have been favored for use in biodistance analysis (e.g., Larsen, 1997;
139 Pietrusewsky, 2000; Stojanowski and Schillaci, 2006) because of the moderate to high degree of heritability
140 (Kieser, 1990; Scott, 1991; Dempsey and Townsend, 2001), absence of remodeling after crown completion,
141 and generally better preservation of the crown (Hillson, 1996; Scott and Turner, 1997). All of the dental

measurements used in this study were collected by one of the authors (W. M.), using digital calipers. Mesiodistal (MD) and buccolingual (BL) measurements were made following the methodology of Fujita (1949). Basically, measurements of the right teeth were used for statistical analyses. However, when the right side tooth was missing, measurements from the left antimere were substituted. Any dental measurement that was potentially affected by dental wear, calculus and caries was treated as missing data. To ensure accuracy, each measurement was made three times, and its mean value was used. The multivariate analyses require a complete data set for each individual, but this is a hard condition to fulfill for Jomon samples because of heavy attrition, tooth ablation, dental caries, and so on. After testing for normality for each measurement, we removed individuals who had too few measurements, and measurements which were taken on too few individuals from the data set to achieve a good balance between the number of samples and that of variables in a stepwise fashion. Finally, we used eight measurements (UP2MD, UP2BL, UM1MD, UM1BL, LP2MD, LP2BL, LM1MD, and LM1BL) from 34 individuals (Table 2).

Before using univariate and multivariate statistical methods, all measurements were size-standardized by a Q-mode correction where each dental measurement was divided by the geometric mean for all the measurements for each individual in the sample (Corruccini, 1973; Darroch and Mosimann, 1985; Powell and Neves, 1999; Scherer, 2007; Temple et al., 2011). To eliminate sex-related size variation while retaining shape variation, geometric means were derived by multiplying together all the variables for each individual and calculating the n th root of this product (n = number of variables for the individual).

Firstly, to examine the association between dental metric variation and the difference of the childhood home based on strontium isotope ratio, all samples were divided into four clusters by K -means clustering of dental measurements (Hartigan and Wong, 1979). Then, these four clusters were fitted to four groups: Yoshigo immigrant, Yoshigo local, Inariyama immigrant, and Inariyama local. The significance of the deviation from a null hypothesis consisting of the absence of contingency between them was evaluated by

Fisher's exact test ($\alpha = 0.05$) since the sample size was small.

Secondly, Principal Component Analysis (PCA) was carried out using size-standardized dental measurements, to examine patterns of phenotypic variability between immigrants and locals based on a human migration model. The principal components (PCs) are ranked by the amount of the total variance that each of them explains. Then, it can be used as a data reduction technique that generates new variables from the original datasets. Individuals that occupy a similar space in the PCA plots are morphologically similar and are considered to be, to some degree, genetically similar because phenotypic covariance, which was calculated from standardized variables for all specimens in the present study, is related to genetic covariance (Chevrud, 1988; Williams-Blangero and Blangero, 1989). After plotting all samples by the first two or three PCA scores, we determined 95% confidence ellipses of Yoshigo and Inariyama locals using a principal axis method (Sokal and Rolf, 1995). This method allowed us to assess whether or not immigrants of each site fell within the range of local dental variations. The results of this method were compared with the estimation of the childhood home based on the strontium isotope data.

If immigrants had originated from multiple populations, the variance of immigrants would be larger than that of locals. To estimate the difference of phenotypic variability between immigrants and locals, both univariate and multivariate data analyses were conducted. For each Q-mode transformed dental metric variable, the difference of within-group variance between immigrants and locals was tested using a univariate F-test (Manly, 1994). Before the F-test, normality was confirmed by the Kolmogorov-Smirnov test ($\alpha = 0.05$). Due to the small sample size, we bootstrapped the sample standard deviations to obtain bias-free estimates of variance (Efron, 1981). The F-test was conducted using variances for all bias-corrected variables.

For multivariate data analysis, the determinant of the variance-covariance matrix was calculated (Green, 1976; Konigsberg, 1988; Schillaci and Stojanowski, 2003). Pair-wise determinant ratios between immigrants and locals were evaluated for statistical significance, using a nonparametric bootstrap method

(Petersen, 2000). The data were resampled (9999 iterations) after random shuffling with sizes equal to the original sample sizes to generate a randomized distribution of determinant ratio values. The P -value was calculated by dividing the number of resampled values greater than or equal to the observed determinant ratio plus one by the number of resamplings plus one (Manly, 1997; Petersen, 2000). The ratio of determinants is supposed to be one when equal mobility between the two groups exists (Konigsberg, 1988). When a numerator group is more mobile, the determinant ratio is positive, and *vice versa*. In this procedure, to avoid generating singular variance-covariance matrices, the number of variables is limited to $n - 1$ variables where n is the sample size of the smallest group. The number of Yoshigo immigrants ($n = 8$), Inariyama immigrants ($n = 3$) and locals ($n = 7$) were equal to or less than that of the eight variables. Then, variable reduction was achieved using a PCA method within Yoshigo and Inariyama samples, respectively. In the case of Yoshigo, the first seven PCA scores, which contributed to 99.9% of the total variance, were utilized for the determinant ratio analysis. In the case of Inariyama, the first two PCA scores, which contributed to 68.8% of the total variance, were used for the determinant ratio analysis. All statistical analyses were carried out using R.2.9.1 (R Development Core Team, 2009).

Results

The classification of individuals derived from K -means clustering is presented in Table 1. Contingency tables between four clusters of dental measurements and four groups based on strontium isotope analysis are presented in Table 3. The results of Fisher's exact test showed that human migration was significantly deviated from the null hypothesis ($P = 0.004$). This finding suggests that the dental metric variation of Yoshigo and Inariyama skeletal remains is significantly explained by human migration among populations in the Atsumi Peninsula area. Thus, human migration between populations had not completely homogenized local gene pools and most of immigrants who had come from other population had different genetic backgrounds from the locals.

The plot of the first three PC scores for the eight variables across all samples is presented in Figures 3 and 4. The first three PCs have eigenvalues greater than 1.0 and account for 74.1% of the total variance. Figure 3 and 4 showed a general trend that immigrants had larger variability and locals had smaller variability. In Figure 3, four out of eight Yoshigo immigrants (No. 316, 333, 349 and 383) and all of immigrants of Inariyama (No. 217, 231 and 241) fell outside the 95% confidence ellipse of each local group. Two of the Yoshigo immigrants (No. 408 and 488) and two of the Inariyama immigrants (No. 217 and 241) were plotted in the confidence ellipses for the Inariyama and Yoshigo local group, respectively. In Figure 4, three of the Yoshigo immigrants (No. 333, 349 and 408) and two Inariyama immigrants (No. 217 and 241) exhibited dental profiles that were beyond the confidence ellipses for the each local group. These two Inariyama immigrants were also fitted well within the dental distribution of the Yoshigo local group. Additionally, one local of Yoshigo (No. 540) was far apart from the confidence ellipses for the other Yoshigo locals. In total, eight out of 11 immigrants were beyond the respective local dental profile for the first three PC scores.

The results of bootstrapped estimates of standard deviations and F-test *P*-value for the Yoshigo population between the immigrants and the locals are presented in Table 4. The immigrants exhibit larger standard deviations for six out of eight variables, and two of these differences were statistically significant. Although it was not true for all of the variables, a general trend of greater immigrant variance was indicated by larger bias-corrected standard deviations for the majority of variables.

The bootstrapped estimates of the within-group standard deviations and F-test *P*-values for the Inariyama population between the immigrants and the locals are presented in Table 5. The greater immigrant variability was also indicated by the larger standard deviations for six out of eight variables, with three of them significant. Larger variability was also observed in Inariyama immigrants.

Table 6 shows the results of determinant ratio analysis as a means of multivariate evaluation of within-group variation between immigrants and locals. The determinant of the variance-covariance matrix

could be utilized as a generalized variance measure (Green, 1976). Generally, a population with a greater number of immigrants will show a large determinant. It was expected that the immigrant group would have a large determinant than its local group, and the determinant ratio between immigrants and locals exceeds 1.0.

The randomization probability indicated a significant departure from a determinant ratio of one at the $\alpha = 0.05$ level for the Yoshigo Shell Mounds. In the case of Inariyama, the determinant ratio exceeded 1.0, and resampling analysis also found significant difference in the amount of variability between the immigrants and the locals. It is concluded that the local group had quite small diversity relative to the immigrant group in both populations (Figures 3 and 4).

Most of the immigrants were excluded from the confidence ellipses of local variation, and the variances of immigrants were significantly larger than those of locals, suggesting that immigrants came from multiple groups which were genetically segregated from each other.

Discussion

This study attempted to clarify inter-population genetic relationships in the Jomon Atsumi Peninsula area by comparing dental morphological variation and human migration patterns. The results of correlation tests revealed that dental metric variations in Yoshigo and Inariyama Shell Mounds were significantly associated with the distinction between immigrants and locals determined from the strontium isotope ratio of the third molar enamel. This result suggested regional genetic heterogeneity among local populations in the Atsumi Peninsula area. Matsumura's (2000) dental metric study on skeletal remains from four sites in the Atsumi Peninsula area revealed that most individuals from these four sites did not form clear site-specific clusters. The results of the present study, however, suggest that the local gene pools had not been totally homogenized but mutual human migration between populations masked morphological distinction.

Excavated human remains may be an aggregate of individuals who lived at different times during the formation of the sites (Pietrusewsky, 2000; Stojanowski and Schillaci, 2006). Actually, most of the sites in the Atsumi Peninsula were formed from the later part of the Late Jomon period to the Final Jomon period (ca. 3500–2300 BP), and both the Yoshigo and Inariyama Shell Mounds lasted for several hundreds years (Yamanouchi, 1952; Sugihara and Toyama, 1964; Kusaka et al., 2009). Observed biological variation can be changed through temporal processes (Owsley et al., 1982; Konigsberg, 1990a, b; Stojanowski, 2003, 2004, 2005a, b). However, the results of the present study indicated that human migration caused intra-site dental variation in the Atsumi Peninsula area. Since immigrants identified by strontium isotope ratio were first generation individuals who had migrated from other populations and the proportion of immigrants was 20–30 % (Kusaka et al., 2009, 2011), the temporal process of biological variation would be less prominent here than the effect of human migration.

PCA showed that five out of eight Yoshigo immigrants and all of the Inariyama immigrants were plotted outside of the confidence ellipses of each local variation. On the whole, the immigrants were scattering more broadly than the locals and the distributions of them were not skewed in both of Yoshigo and Inariyama population, suggesting that the immigrants did not share a common dental morphology. Furthermore, No. 540 was an outlier of the local Yoshigo distribution (Figure 4). Kusaka et al. (2009) raised the possibility that this individual, with strontium isotope ratio close to the low end of the local variation, actually might have been an immigrant from the eastern inland area. The dental profile of No.540 that was beyond the Yoshigo local dental distribution would support this possibility.

All three Inariyama immigrants were outliers from the local dental variation. In the case for Inariyama, the local variation is small and outliers are more clearly identified. In this study, human migration presumed from isotope ratio was significantly associated with dental variation, and local individuals showed close morphological similarities each other in the PCA plots. Low dental variability of the Inariyama local population relative to the Yoshigo locals might be explained from either a greater effect of migration due to

the longer duration of Yoshigo Shell Mounds, or a presence of a greater number of hidden immigrants. In any case, it is concluded that Inariyama locals showed relatively high genetic similarity among their small population.

The evaluation of dental variability in the local and immigrant groups leads to a plausibility of multiple origins of the immigrants. The results of the univariate analyses of between immigrants and locals within the Yoshigo and Inariyama Shell Mounds revealed a tendency of greater immigrant variation. The multivariate determinant ratio analyses also seemed to support these univariate results in both of the sites. It is important to note that those immigrants did not share a common dental morphology according to the PCA, and that the variance of the immigrants was significantly larger than that of the locals in both univariate and multivariate variance comparisons. This suggested that these immigrants had come from multiple parent populations, and these genetically distinct groups interacted with each other within and outside the Atsumi Peninsula area.

In general, migration among demes is considered to retard genetic differentiation. Therefore, the regional heterogeneity among the populations observed in the present study might have been caused by a lack of frequent interaction, insufficient duration for genetic admixture, or both of them. Regional genetic variation is expected to be high when local populations are relatively non-mobile and inter-population gene flow is restricted due to geographical or social/cultural barriers. However, it seems unlikely that there were such barriers or infrequent gene flow in the relatively narrow Atsumi Peninsula area. In relatively small-scale, low density, and kin-based societies where families migrate frequently, such as the Yanomamo of South America or the Semai of Malaysia, it has been shown that kin-structured migration increases genetic variation among populations (Fix, 1975, 1978, 1999, 2004; Smouse et al, 1981). Groups of kin hive off from local settlements to fuse with another population or establish new settlements of their own. Such a migrant group shares similar genotypes leading to biological relatedness, so that kin-structured migration can affect gene frequencies of both donor and recipient populations in smaller societies (Fix, 2004).

Williams-Blangero (1989a, b) and Williams-Blangero and Blangero (1989) also found significant anthropometric microdifferentiation between villages of the Jirel of Nepal despite migration among them, which might have been caused by nonrandom marital migration (clan-structured migration) related to kin-structured migration. It is conceivable that a similar mechanism has worked to establish microdifferentiation among the Jomon populations in the Atsumi Peninsula area. Interpopulation differentiation caused by nonrandom kin-structured migration can be seen in not only the Yanomamo and the Semai, which depend on swidden gardens for subsistence (Dentan, 1968; Neel, 1978; Fix, 1999), but also the Jirel, which is settled agriculturalist lived in restricted region (Bista, 1996). Although it is uncertain to what extent these populations can be analogous for Jomon people, who were sedentary hunter-gatherer, microdifferentiation among populations would result from nonrandom kin-structured migration upon marriage, and/or for fusing another groups or establishing new settlements. Jomon people in the Atsumi Peninsula area might have had a social organization in which kinship played a major role as social glue.

In the Jomon period, there were two cooling trends (Sakaguchi, 1989; Umitsu, 1994). The second cooling and fall of the sea level occurred during the Final Jomon period (Izeki, 1974; Ota et al., 1982, 1990; Umitsu, 1994), leading to a further reduction of the Jomon population throughout most of the Japanese Archipelago (Koyama, 1978; Koyama and Sugito, 1984). However, in Aichi prefecture, the number and scale of the sites increased from the Late to Final Jomon period (Koyama, 1978). Settlements in the Atsumi Peninsula area might have benefitted from access to shellfish in tidelands after the marine regression (Masuko, 1980; Iwase, 1991). In contrast, in the western part of the Aichi prefecture (Owari region) traces of human activity markedly decreased, suggesting a drastic population decline (Koumura, 1981; Masuko, 2001, 2006). These demographic changes may suggest population movements to the Atsumi Peninsula area from neighboring areas (Masuko, 1980). Immigrants identified by strontium isotope analysis were members of the first generation who had migrated from distinct populations, and their genetic traits were different from those of each other and those of local populations. The parent populations of most of immigrants

analyzed in the present study had not been included in the gene pools of each local population which had been constituted by interaction with other populations until then. Several researchers have suggested the possibilities that extraregional gene flow and migration, and/or population aggregation increased intracemetery heterogeneity (Key and Jantz, 1990; Griffin et al., 2001; Stojanowski, 2003, 2005b; Schillaci and Stojanowski, 2005). The present study could not verify the temporal change of genetic variation, and it may be conceivable that relatively high intrapopulation relatedness and migration among the surrounding and extraregional populations had occurred without environmental change. However, the biological and archaeological findings here suggested that not only extraregional gene flow, but also the population aggregation from the surrounding areas associated with the climatic change of the Late to the Final Jomon period might have caused multiple genetically distinct populations to congregate in the Atsumi Peninsula area.

Conclusion

We investigated whether inter-population genetic relationships in the Jomon Atsumi Peninsula area were homogeneous or heterogeneous, by combining dental metric and strontium isotope data about migratory patterns to investigate the population structure of the prehistoric society. The results showed that human migration patterns based on strontium isotope analysis were significantly correlated with dental metric variation, suggesting regional genetic heterogeneity between local populations. Although the difference of childhood home of Yoshigo and Inariyama individuals based on strontium isotope analysis did not completely correspond with the dental variability from PCA, at least eight of 11 identified immigrants exhibited dental profiles atypical of each local variation. The variances of the immigrants were significantly larger than those of the locals, suggesting multiple origins of the immigrants. Microdifferentiation among populations in this area would have resulted from nonrandom kin-structured migration in the relatively small-scale, low-density, and kin-based societies as seen in the Yanomamo, the Semai or the Jirel

populations, and/or population aggregation from surrounding areas in accordance with climatic change in the Final Jomon period.

We found regional heterogeneity among Jomon populations in the Atsumi Peninsula area, and reconstructed population dynamics in a temporally constrained small region by means of combination analysis of the spatial variance of childhood home based on strontium isotope analysis and phenotypic variance as a proxy for genetic variation, with full consideration of the archaeological context. This study shows the usefulness of combining the phenotypic approach and the geochemical method for the reconstruction of prehistoric human societies in more detail.

Acknowledgments

The authors wish to thank to Professor Emeritus K. Katayama (Kyoto University), and members of the Laboratory of Physical Anthropology, Kyoto University for helpful discussions and comments, especially to C. Ramos for correcting the manuscript. We also thank Dr. T. Nagaoka (St. Marianna University School of Medicine) and Prof. T. Hanihara (Kitasato University School of Medicine), for their thoughtful advises and comments on this study. Finally, we would like to thank two anonymous reviewers for their insightful comments and positive criticisms of our original manuscript. This study was supported in part by the Global COE Program A06 to Kyoto University.

References

- Adachi N., Dodo Y., Ohshima N., Doi N., Yoneda M., and Matsumura H. (2003) Morphologic and genetic evidence for the kinship of juvenile skeletal specimens from a 2,000 years-old double burial of the Usu-Moshiri site, Hokkaido, Japan. *Anthropological Science*, 111: 347–363.
- Adachi N., Suzuki T., Sakaue K., Takigawa W., Ohshima N., and Dodo Y. (2006) Kinship analysis of the Jomon skeletons unearthed from a double burial at the Usu-Moshiri site, Hokkaido, Japan.

- 382 Anthropological Science, 114: 29–34.
- 383 Bentley R.A. (2006) Strontium isotopes from the earth to the archaeological skeleton: a review. *Journal of*
- 384 *Archaeological Method and Theory*, 13: 135–187.
- 385 Bentley R.A., Buckley H.R., Spriggs M., Bedford S., Ottley C.J., Nowell G.M., Macpherson C.G., and
- 386 Pearson D.G. (2007) Lapita migrants in the Pacific's oldest cemetery: isotopic analysis at Teouma,
- 387 Vanuatu. *American Antiquity*, 72: 645–656.
- 388 Bista D.B. (1996) *People of Nepal*. Ranta Pustak Bhandar, Kathmandu.
- 389 Buikstra J.E., Frankenberg S.R., and Konigsberg L.W. (1990) Skeletal biological distance studies in
- 390 *American Physical Anthropology: recent trends*. *American Journal of Physical Anthropology*, 82: 1–7.
- 391 Chevrud J. (1988) A comparison of genetic and phenotypic correlations. *Evolution*, 42: 958–968.
- 392 Chisholm B. and Koike H. (1999) Reconstructing prehistoric Japanese diet using stable isotopic analysis,
- 393 *Interdisciplinary perspectives on the origins of the Japanese*. In: Omoto K. (ed.), *Interdisciplinary*
- 394 *Perspectives on the Origins of the Japanese*. International Research Center for Japanese Studies, Kyoto,
- 395 pp. 69–73.
- 396 Corruccini R.S. (1973) Size and shape in similarity coefficients based on metric characters. *American*
- 397 *Journal of Physical Anthropology*, 38: 743–753.
- 398 Darroch J.N. and Mosimann J.E. (1985) Canonical and principal components of shape. *Biometrika*, 72:
- 399 241–252.
- 400 Dempsey P.J. and Townsend G.C. (2001) Genetic and environmental contributions to variation in human
- 401 tooth size. *Heredity*, 86: 685–693.
- 402 Dentan R.K. (1968) *The Semai: A Nonviolent People of Malaya*. Holt, Rinehart and Winston, New York.
- 403 Efron B. (1981) Censored data and the bootstrap. *Journal of the American Statistical Association*, 76:
- 404 312–319.
- 405 Ezzo J.A., Johnson C.M., and Price T.D. (1997) Analytical perspectives on prehistoric migration: a case

- 406 study from east-central Arizona. *Journal of Archaeological Science*, 24: 447–466.
- 407 Fix A.G. (1975) Fission-fusion and lineal effect: aspects of the population structure of the Semai Senoi of
408 Malaysia. *American Journal of Physical Anthropology*, 43: 295–302.
- 409 Fix A.G. (1978) The role of kin-structured migration in genetic microdifferentiation. *Annals of Human*
410 *Genetics*, 41: 329–339.
- 411 Fix A.G. (1999) *Migration and Colonization in Human Microevolution*. Cambridge University Press,
412 Cambridge.
- 413 Fix A.G. (2004) Kin-structured migration: Causes and consequences, *American Journal of Human Biology*,
414 16: 387–394.
- 415 Fujita T. (1949) On the standard of the measurement of teeth. *Journal of the Anthropological Society of*
416 *Nippon*, 61: 27-32 (in Japanese).
- 417 Funahashi K. (2008) Tooth ablation [Basshi]. In: Kosugi Y., Nishida Y., Mizunoe K., Taniguchi Y., and
418 Yano K. (eds.), *Human and Society [Hito to shakai]*. Douseisha, Tokyo, pp. 194–206 (in Japanese).
- 419 Green P.E. (1976) *Mathematical Tools for Applied Multivariate Analysis*. Academic Press, New York.
- 420 Griffin M.C., Lambert P.M. and Monahan-Driscoll E. (2001) Biological relationships and population
421 history of native peoples in Spanish Florida and the American Southeast. In: Larsen C.S. (ed.),
422 *Bioarchaeology of Spanish Florida: the Impact of Colonialism*. University Press of Florida, Gainesville,
423 pp. 226–273.
- 424 Habu J. (2004) *Ancient Jomon of Japan*, Cambridge University Press, Cambridge.
- 425 Hartigan J.A. and Wong M.A. (1979) Algorithm AS 136: A K-means clustering algorithm. *Applied*
426 *Statistics*, 28: 100–108.
- 427 Harunari H. (1979) Postmarital modes of residence of the Final Jomon period [Jomon banki no kongo
428 kyoju kitei]. *Journal of Faculty of Law and Literature of Okayama University [Okayama daigaku*
429 *houbungakubu gakujyutsu kiyou]*, 40: 25–63 (in Japanese).

- 430 Harunari H. (1986) Rules of residence in the Jomon period based on the analysis of tooth extraction. In:
- 431 Pearson R.J., Barnes G.L., and Hutterer K.L. (ed.), *Windows on the Japanese Past: Studies in*
- 432 *Archaeology and Prehistory*, Center for Japanese Studies, University of Michigan, pp. 293–310.
- 433 Hayden B. (1995) Pathways to power: principles for creating socioeconomic inequalities. In: Price T. D. and
- 434 Feinman G.M. (eds.), *Foundation of Social Inequality*. Plenum Press, New York, pp. 15–86.
- 435 Hillson S. (1996) *Dental Anthropology*. Cambridge University Press, Cambridge.
- 436 Imamura K. (1996a) *Prehistoric Japan: New Perspectives on Insular East Asia*. University of Hawaii Press,
- 437 Honolulu.
- 438 Imamura K. (1996b) Jomon and Yayoi: the transition to agriculture in Japanese prehistory. In: Harris D.R.
- 439 (ed.) *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. Smithsonian Institution Press,
- 440 Washington, pp. 442–464.
- 441 Iwase A. (1991) Sea-level change and shell mounds transition [Kaimen hendo to kaiduka no henshen]. In
- 442 School Board of Toyohashi City (ed.), *The Ichikisima jinja Site (I) [Ichikisima jinja iseki (I)]*. School
- 443 Board of Toyohashi City, Aichi, pp. 75–78 (in Japanese).
- 444 Izeki K. (1974) The sea level around 2000B.P. in Japan [Nihon ni okeru 2000nen B.P. korono kaisuijun].
- 445 *Journal of the faculty of letters, Nagoya University, History [Nagoya daigaku bungakubu kenkyu*
- 446 *ronshu (Shigaku)]*, 21: 1–22 (in Japanese).
- 447 Key P.J. and Jantz R.L. (1990) Statistical assessment of population variability: a methodological approach.
- 448 *American Journal of Physical Anthropology*, 82: 53–59.
- 449 Kieser J.A. (1990) *Human Adult Odontometrics: the Study of Variation in Adult Tooth Size*. Cambridge
- 450 University Press, Cambridge.
- 451 Kiyono K. (1925) A study of primitive people in Japan [Nihon genjin no kenkyu]. Okashoin, Tokyo (in
- 452 Japanese).
- 453 Kiyono K. (1928) A study of the Stone Age Japanese [Nihon sekkijidaijin kenkyu], Okashoin, Tokyo (in

- 454 Japanese).
- 455 Kiyono K. (1969) Studies of Japanese Shell Mounds [Nihon kaizuka no kenkyu]. Iwanami-shoten, Tokyo
- 456 (in Japanese).
- 457 Knudson K.J. and Price T.D. (2007) Utility of multiple chemical techniques in archaeological residential
- 458 mobility studies: case studies from Tiwanaku-and Chiribaya-affiliated sites in the Andes. American
- 459 Journal of Physical Anthropology, 132: 25–39.
- 460 Kobayashi T., Kaner S., and Nakamura O. (2004) Jomon Reflection: Forager Life and Culture in the
- 461 Prehistoric Japanese Archipelago. Oxbow Books, Oxford.
- 462 Kondo O. (1994) The skulls of Ubayama shell-mounds II. An analysis of intra-and inter-regional variation
- 463 of the Jomon population. Anthropological Science, 102: 59–74.
- 464 Konigsberg L.W. (1988) Migration models of prehistoric postmarital residence. American Journal of
- 465 Physical Anthropology, 77: 471–482.
- 466 Konigsberg, L.W. (1990a) Analysis of prehistoric biological variation under a model of isolation by
- 467 geographic and temporal distance. Human Biology, 62: 49–70.
- 468 Konigsberg, L.W. (1990b) Temporal aspects of biological distance: serial correlation and trend in a
- 469 prehistoric skeletal lineage. American Journal of Physical Anthropology, 82: 45–52.
- 470 Konigsberg L.W. and Buikstra J.E. (1995) Regional approaches to the investigation of past human
- 471 biocultural structure, In: Beck L. (ed.), Regional Approaches to Mortuary Analysis. Plenum Press, New
- 472 York, pp. 191–219.
- 473 Koumura H. (1981) The various stages of prehistoric culture in the Tokai region [Tokai senshi bunka no
- 474 shodankai]. printed as manuscript (in Japanese).
- 475 Koyama S. (1978) Jomon subsistence and population. Senri Ethnological Studies, 2: 1–65.
- 476 Koyama S. and Sugito S. (1984) A study of Jomon population—computer simulation analysis [Jomon jinko
- 477 simulation]. Bulletin of the National Museum of Ethnology, 9: 1–39.

- 478 Kusaka S., Ikarashi T., Hyodo F., Yumoto T., and Katayama K. (2008) Variability in stable isotope ratios in
479 two Late-Final Jomon communities in the Tokai coastal region and its relationship with sex and ritual
480 tooth ablation. *Anthropological Science*, 116: 171–181.
- 481 Kusaka, S., Ando A., Nakano T., Yumoto T., Ishimaru E., Yoneda M., Hyodo F., and Katayama K. (2009) A
482 strontium isotope analysis on the relationship between ritual tooth ablation and migration among the
483 Jomon people in Japan. *Journal of Archaeological Science*, 36: 2289–2297.
- 484 Kusaka S., Nakano T., Yumoto T., and Nakatsukasa M. (2011) Strontium isotope evidence of migration and
485 diet in relation to ritual tooth ablation: A case study from the Inariyama Jomon site, Japan. *Journal of*
486 *Archaeological Science*, 38: 166–174.
- 487 Lane R.A. and Sublett A.J. (1972) Osteology of social organization: Residence pattern. *American Antiquity*,
488 37: 186–201.
- 489 Larsen C.S. (1997) *Bioarchaeology: Interpreting Behavior from the Human Skeleton*. Cambridge
490 University Press, Cambridge.
- 491 Larsen C.S. (2002) *Bioarchaeology: the lives and lifestyles of past people*. *Journal of Archaeological*
492 *Research*, 10: 119–166.
- 493 Manly B.F. (1994) *Multivariate Statistical Methods: A Primer*, 2nd ed. Chapman and Hall, London.
- 494 Manly B.F. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman and Hall,
495 London.
- 496 Masuko Y. (1980) A revisional study of last phase of the Late period and the Final period Jomon culture in
497 the eastern Mikawa region (II) [Higashi mikawa ni okeru Jomon koukimatsu banki bunka no saikento
498 (II)]. *Bulletin of the Nagoya Archaeological Society [Kodaijin]*, 36: 13–24 (in Japanese).
- 499 Masuko Y. (2001) Various aspects of Jomon settlements in the Aichi prefecture [Aichiken ni okeru Jomon
500 jidai shuraku no shoyousou]. In: *Society for the cultural study of the Jomon period*. (ed.), Various
501 aspects of Jomon Settlements in the Japanese Archipelago [Retto ni okeru Jomon jidai shuraku no

- shoyousou]. Society for the Cultural Study of the Jomon Period, Tokorozawa, pp. 451–468.
- Masuko Y. (2006) The transition from Kaminari II pottery style to Sakurai and Inariyama pottery style [Kaminari II shiki kara sakurai shiki inariyama shiki heno iko]. Bulletin of the Nagoya Archaeological Society [Kodaijin], 66: 45–63.
- Matsumura H. (2000) Dental Metric Variations between the Periods, Sites and Individuals of the Neolithic Jomon People in the Setouchi, Tokai, and Kanto Regions, Japan, Memoirs of the National Science Museum, Tokyo, 32: 175–187 (in Japanese with English summary).
- Matsumura H., Ishida H., and Hashimoto H. (1996) Cranial and dental traits of the Nakazuma Jomon people from Ibaraki, Japan. Bulletin of the National Science Museum, Tokyo, D22: 1–26.
- Matsumura H. and Nishimoto T. (1996) Statistical analysis on kinship of the Nakazuma Jomon people using tooth crown measurements. Zoo-archaeology, 6: 1–17 (in Japanese with English summary).
- Montgomery J., Evans J.A., and Cooper R.E. (2007) Resolving archaeological populations with Sr-isotope mixing models. Applied Geochemistry, 22: 1502–1514.
- Neel J.V. (1978) The population structure of an Amerindian tribe, the Yanomama. Annual Review of Genetics, 12: 365–413.
- Ota Y., Matsushima Y., and Moriwaki H. (1982) Notes on the Holocene sea-level study in Japan — on the basis of ‘Atlas of Holocene sea-level records in Japan’ —. The Quaternary Research, 21: 133–143 (in Japanese, with English summary).
- Ota Y., Umitsu M., and Matsushima Y. (1990) Recent Japanese research on relative sea level changes in the Holocene and related problems — review of studies between 1980 ~ 1988 —. The Quaternary Research, 29: 31–48 (in Japanese, with English summary).
- Owsley, D.W., Bennett, S.M. and Jantz, R.L. (1982) Intercemetery morphological variation in Arikara crania from the Mobridge site (39WW1). American Journal of Physical Anthropology, 58: 179–185.
- Petersen H.C. (2000) On statistical methods for comparison of intrasample morphometric variability:

- 526 Zalavár revisited. *American Journal of Physical Anthropology*, 113: 79–84.
- 527 Pietrusewsky M. (2000) Metric analysis of skeletal remains: methods and applications. In: Katzenberg M.A.
- 528 and Saunders S.R. (eds.), *Biological Anthropology of the Human Skeleton*. Wiley-Liss, New York, pp.
- 529 375–415.
- 530 Powell J.F. and Neves W.A. (1999) Craniofacial morphology of the first Americans: Pattern and process in
- 531 the peopling of the New World. *Yearbook of Physical Anthropology*, 42: 153–188.
- 532 Price T.D., Burton J.H., and Bentley R.A. (2002) The characterization of biologically available strontium
- 533 isotope ratios for the study of prehistoric migration. *Archaeometry*, 44: 117–135.
- 534 R Development Core Team. (2009) R: a Language and Environment for Statistical Computing. R
- 535 Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- 536 Sakaguchi Y. (1989) *The Natural History of Ozegahara [Ozegahara no shizenshi]*. Chuoukouronsha, Tokyo
- 537 (in Japanese).
- 538 Scherer A.K. (2007) Population structure of the Classic period Maya. *American Journal of Physical*
- 539 *Anthropology*, 132: 367–380.
- 540 Schillaci M.A. and Stojanowski C.M. (2003) Postmarital residence and biological variation at Pueblo
- 541 Bonito. *American Journal of Physical Anthropology*, 120: 1–15.
- 542 Schillaci M.A. and Stojanowski C.M. (2005) Craniometric variation and population history of the
- 543 prehistoric Tewa. *American Journal of Physical Anthropology*, 126: 404–412.
- 544 Scott G. R., 1991, Dental anthropology. In: Dulbecco R. (ed.), *Encyclopedia of Human Biology*, San
- 545 Diego ; Tokyo, Academic Press, vol. . 2 : Br-De, p. 789–804.
- 546 Scott G.R. and Turner C.G. (1997) *The Anthropology of Modern Human Teeth*. Cambridge University
- 547 Press, Cambridge.
- 548 Shinoda K., Matsumura H., and Nishimoto T. (1998) Genetical and morphological analysis on kinship of
- 549 the Nakazuma Jomon people using mitochondrial DNA and tooth crown measurements.

- 550 Zoo-archaeology, 11: 1–21 (in Japanese).
- 551 Smouse P.E., Vitzthum V.J., and Neel J.V. (1981) The impact of random and lineal fission on the genetic
552 divergence of small human groups: a case study among the Yanomama. *Genetics*, 98: 179–191.
- 553 Sokal R.R. and Rohlf F. J. (1995) *Biometry*, 3rd ed. WH Freeman, New York.
- 554 Spence M.W. (1974) Residential practices and the distribution of skeletal traits in Teotihuacan, Mexico.
555 *Man*, 9: 262–273.
- 556 Stojanowski C.M. (2003) Differential phenotypic variability among the Apalachee populations of La
557 Florida: A diachronic perspective. *American Journal of Physical Anthropology*, 123: 316–332.
- 558 Stojanowski C.M. (2004) Population history of native groups in pre- and postcontact Spanish Florida:
559 Aggregation, gene flow, and genetic drift on the Southeastern US Atlantic coast. *American Journal of*
560 *Physical Anthropology*, 123: 316–332.
- 561 Stojanowski C.M. (2005a) The bioarchaeology of identity in Spanish colonial Florida: Social and
562 evolutionary transformation before, during, and after demographic collapse. *American Anthropologist*,
563 107: 417–431.
- 564 Stojanowski C.M. (2005b) Spanish colonial effects on Native American mating structure and genetic
565 variability in northern and central Florida: evidence from Apalachee and western Timucua. *American*
566 *Journal of Physical Anthropology*, 128: 273–286.
- 567 Stojanowski C.M. and Schillaci M.A. (2006) Phenotypic approaches for understanding patterns of
568 intracemetery biological variation. *American Journal of Physical Anthropology*, 43: 49–88.
- 569 Sugihara S. and Toyama K. (1964) Sites along the Toyo-river in the Final Jomon Period [Toyogawa kayuiki
570 niokeru Jomon jidai banki no iseki]. *Kokogaku-shukan*, 2: 37–101 (in Japanese).
- 571 Takahashi R. (2004) The front line of the study of Jomon Culture [Jomon bunka kenkyu no saizensen].
572 Waseda University, Tokyo (in Japanese).
- 573 Tanaka Y. (2001) Reconstructing Final Jomon post-marital residential patterns in western Japan. *Bulletin of*

- 574 the Indo-Pacific Prehistory Association, 21: 43–48.
- 575 Temple D.H. (2007) Dietary variation and stress among prehistoric Jomon foragers from Japan. *American*
- 576 *Journal of Physical Anthropology*, 133: 1035–1046.
- 577 Temple D.H., Kusaka S., and Sciulli P.W. (2011) Patterns of social identity in relation to tooth ablation
- 578 among prehistoric Jomon foragers from Yoshigo site, Aichi Prefecture, Japan. *International Journal of*
- 579 *Osteoarchaeology*, 21: 323–335.
- 580 Tsude H. (2001) Yayoi farmers reconsidered: new perspectives on agricultural development in East Asia.
- 581 *Bulletin of the Indo-Pacific Prehistory Association*, 5: 53–59.
- 582 Umitsu M. (1994) Late Quaternary Environment and Landform Evolution of Riverine Coastal Lowlands,
- 583 Kokonshoin, Tokyo (in Japanese).
- 584 Watanabe H. (1990) Jomon Stratified Society [Jomon kaisouka shakai]. Rokuichi-shobo, Tokyo (in
- 585 Japanese).
- 586 Williams-Blangero S. (1989a) Clan-structured migration and phenotypic differentiation in the Jirels of
- 587 Nepal. *Human biology*, 61: 143–157.
- 588 Williams-Blangero S. (1989b) Phenotypic consequences of nonrandom migration in the Jirels of Nepal.
- 589 *American Journal of Physical Anthropology*, 80: 115–125.
- 590 Williams-Blangero S. and Blangero J. (1989) Anthropometric variation and the genetic structure of the
- 591 Jirels of Nepal. *Human biology*, 61: 1–12.
- 592 Yamanouchi S. (1952) The second trench, In: The commission for the protection of cultural properties
- 593 Japan (ed.), *The Shell Mounds of Yoshigo* [Yoshigo kaiduka]. The Commission for the Protection of
- 594 Cultural Properties Japan, Tokyo. pp. 93–124.
- 595
- 596

597 **Figure legends**

598 Figure 1. Map of the study area showing the location of the Yoshigo and Inariyama Shell Mounds.

599

600 Figure 2. Strontium isotope ratios of Yoshigo and Inariyama individuals. The gray horizontal range indicates
601 the local range for Yoshigo (0.7086–0.7092) and Inariyama (0.7091–0.7100). The value of No. 231
602 (0.7066) was changed to shorten the scale. Data from Kusaka et al. (2009, 2011).

603

604 Figure 3. First and second principal components plot of all samples and ninety-five percent confidence
605 ellipses for Yoshigo and Inariyama locals using eight Q-mode corrected variables.

606

607 Figure 4. First and third principal components plot of all samples and ninety-five percent confidence ellipses
608 for Yoshigo and Inariyama locals using eight Q-mode corrected variables.

609

Figure 1.

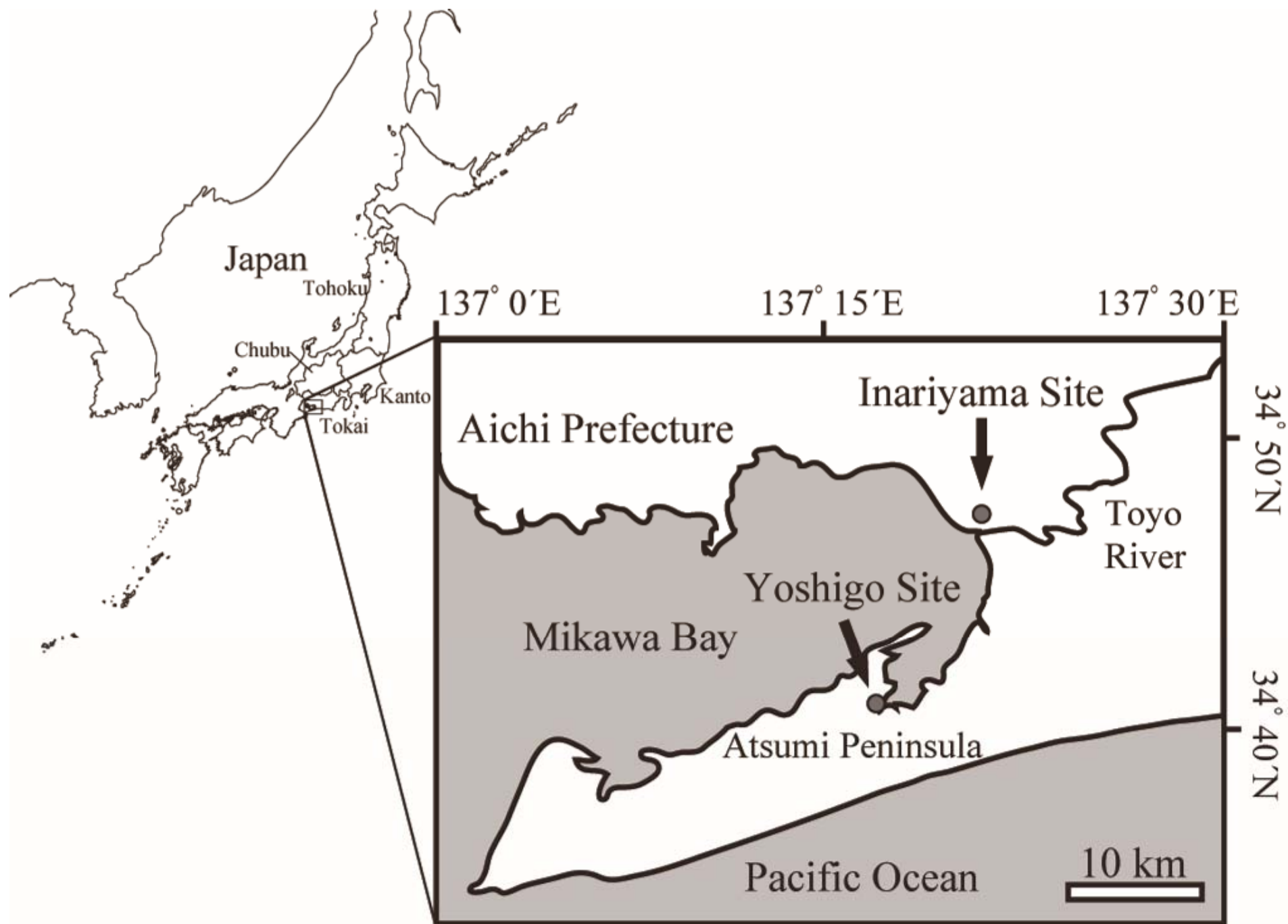


Figure 2.

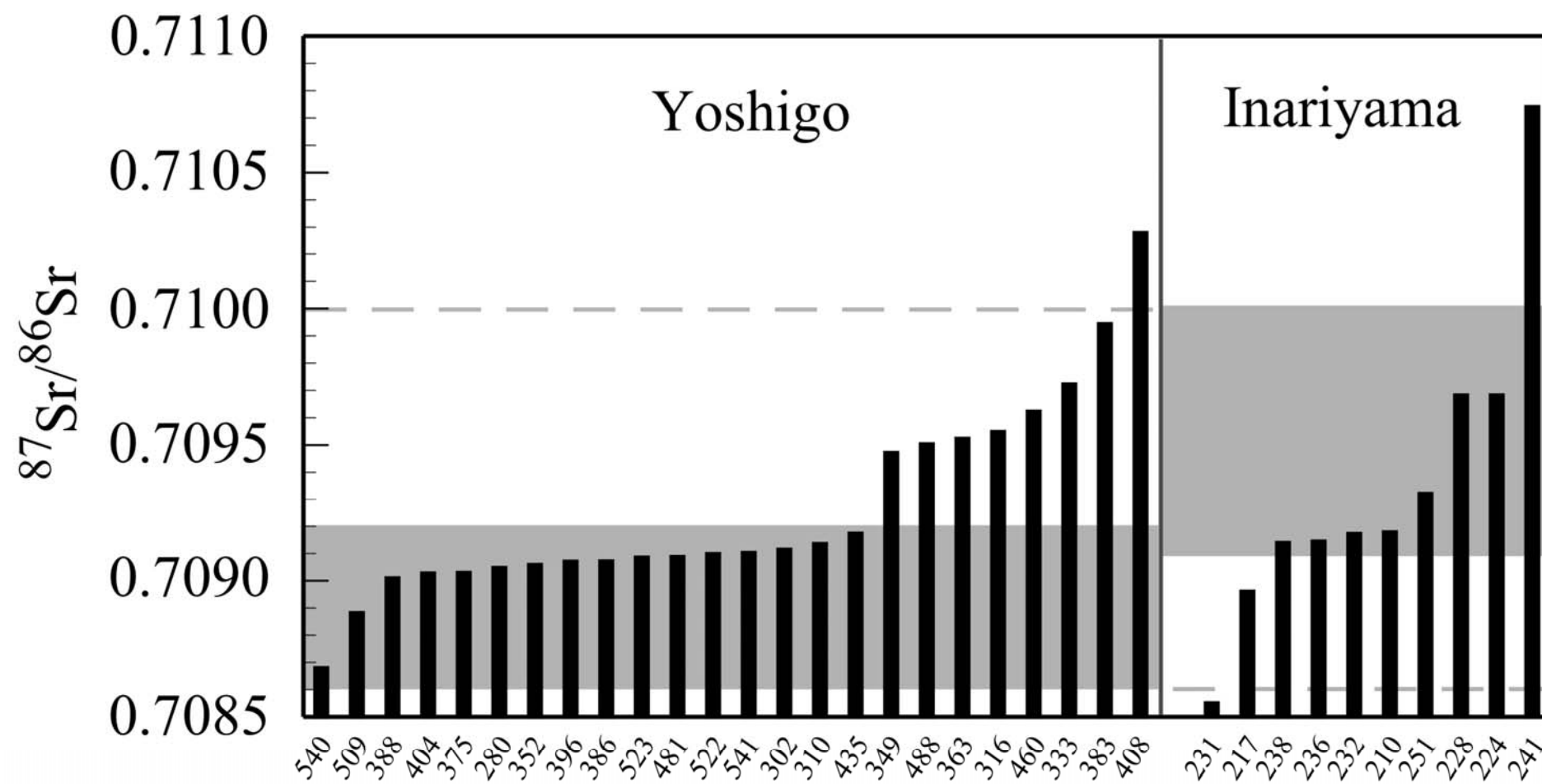


Figure 3.

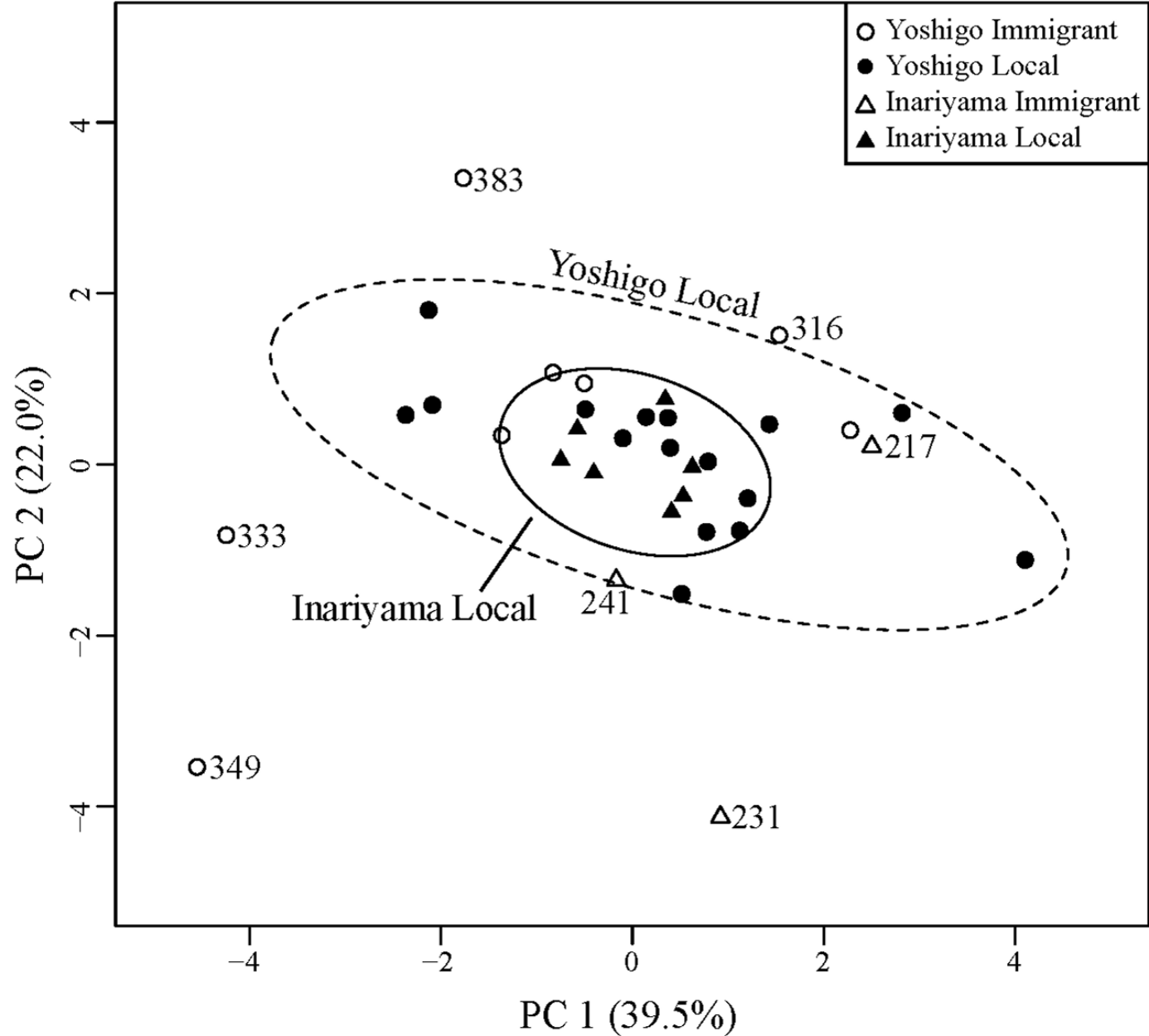


Figure 4.

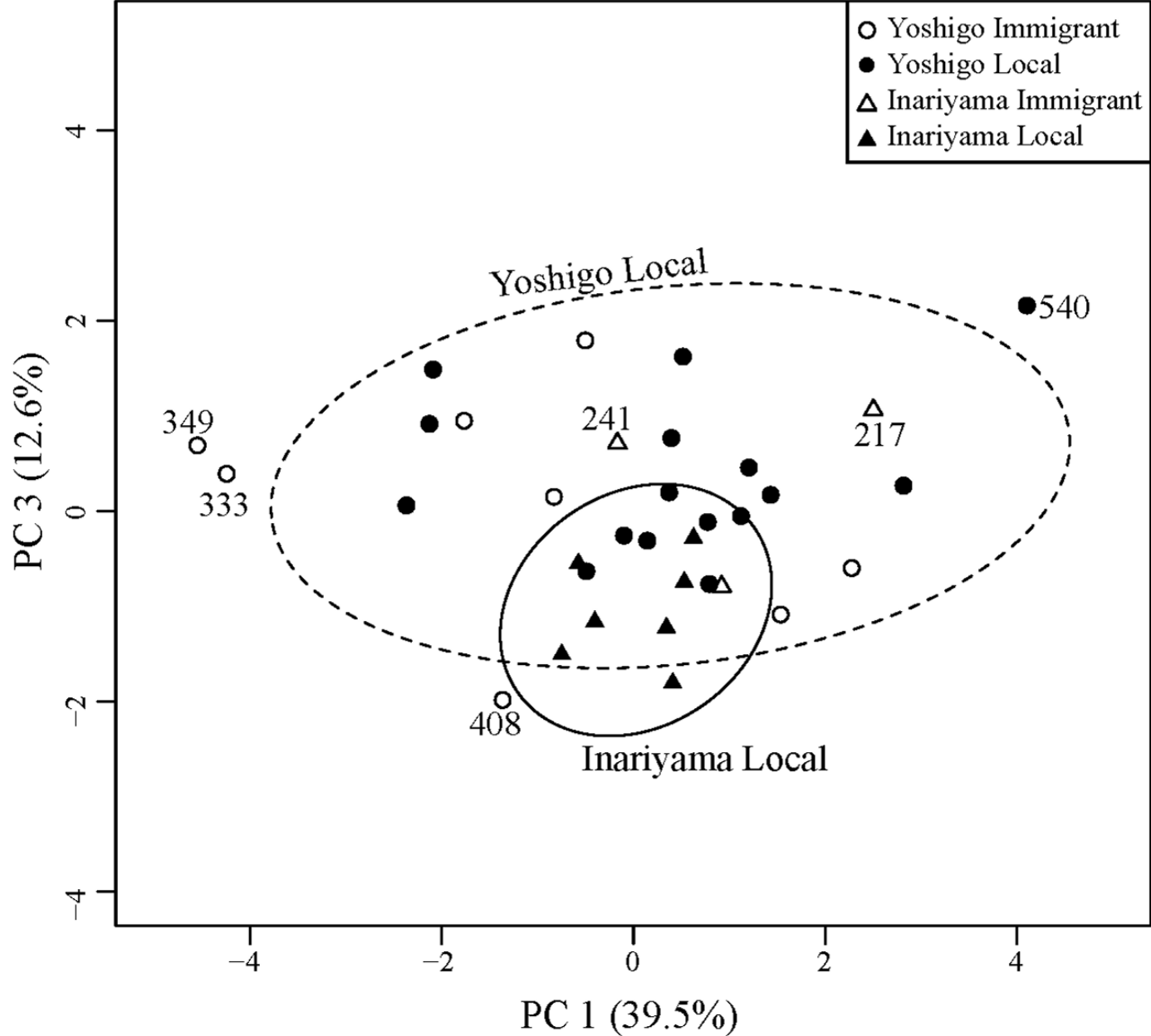


Table 1. Yoshigo and Inariyama human skeletal remains used in this study

Sample No.	Sex	Age at death	Local vs. immigrant ¹	K-means clustering	Individual location in Figure 3	Individual location in Figure 4
Yoshigo Shell Mound						
280	Male	Adolescent	Local	4	Yoshigo ²	Yoshigo ²
302	Female	Young adult	Local	3	Yoshigo	Yoshigo
310	Female	Young adult	Local	4	Yoshigo ²	Yoshigo ²
316	Male	Young adult	Immigrant	2	Outlier	Yoshigo
333	Male	Young adult	Immigrant	1	Outlier	Outlier
349	Male	Young adult	Immigrant	1	Outlier	Outlier
352	Female	Adolescent	Local	2	Yoshigo ²	Yoshigo ²
363	Male	Middle adult	Immigrant	3	Yoshigo	Yoshigo
375	Male	Young adult	Local	2	Yoshigo ²	Yoshigo ²
383	Male	Middle adult	Immigrant	3	Outlier	Yoshigo
386	Male	Young adult	Local	3	Yoshigo	Yoshigo
388	Male	Young adult	Local	2	Yoshigo ²	Yoshigo
396	Male	Young adult	Local	2	Yoshigo	Yoshigo
404	Female	Adolescent	Local	4	Yoshigo ²	Yoshigo ²
408	Female	Adult	Immigrant	4	Yoshigo ²	Outlier
435	Male	Young adult	Local	2	Yoshigo ²	Yoshigo ²
460	Female	Young adult	Immigrant	2	Yoshigo	Yoshigo
481	Male	Middle adult	Local	2	Yoshigo	Yoshigo
488	Female	Middle adult	Immigrant	3	Yoshigo ²	Yoshigo
509	Male	Middle adult	Local	3	Yoshigo	Yoshigo
522	Female	Young adult	Local	2	Yoshigo ²	Yoshigo
523	Female	Young adult	Local	2	Yoshigo ²	Yoshigo ²
540	Female	Middle adult	Local	2	Yoshigo	Outlier
541	Female	Young adult	Local	2	Yoshigo	Yoshigo
Inariyama Shell Mound						
210	Unknown	Adolescent	Local	4	Inariyama	Inariyama
217	Female	Young adult	Immigrant	2	Outlier ³	Outlier ³
224	Female	Middle adult	Local	4	Inariyama	Inariyama
228	Female	Adolescent	Local	4	Inariyama	Inariyama
231	Male	Young adult	Immigrant	2	Outlier	Inariyama
232	Male	Young adult	Local	4	Inariyama	Inariyama
236	Male	Adolescent	Local	4	Inariyama	Inariyama
238	Male	Young adult	Local	4	Inariyama	Inariyama
241	Male	Middle adult	Immigrant	2	Outlier ³	Outlier ³
251	Male	Young adult	Local	2	Inariyama	Inariyama

¹ based on strontium isotope analysis (Kusaka et al., 2009, 2011)

² and also included in dental distribution for Inariyama local

³ and also included in dental distribution for Yoshigo local

Table 2. Mean and standard deviation of the dataset

	UP2MD		UP2BL		UM1MD		UM1BL		LP2MD		LP2BL		LM1MD		LM1BL	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Yoshigo	6.46	0.35	8.97	0.56	10.15	0.50	11.95	0.50	6.92	0.42	8.26	0.50	11.55	0.51	11.12	0.48
Inariyama	6.58	0.28	8.88	0.25	10.32	0.47	11.59	0.37	7.07	0.40	8.40	0.44	11.64	0.49	11.22	0.65
Total	6.49	0.33	8.94	0.49	10.20	0.49	11.84	0.49	6.97	0.41	8.30	0.48	11.57	0.50	11.15	0.52

Table 3. Four by four contingency table consisting of four clusters derived from K -means clustering and four groups based on strontium isotope

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Total
Yoshigo Immigrant	2	2	3	1	8
Yoshigo Local	0	10	3	3	16
Inariyama Immigrant	0	3	0	0	3
Inariyama Local	0	1	0	6	7
Total	2	16	6	10	34

Fisher's exact test, $P = 0.004$

Table 4. Univariate variance tests for Yoshigo population

Variable	Immigrant (n = 8)			Local (n = 16)			F-value	P-value	
	SD	Boot	Bias	SD	Boot	Bias			
UP2MD	0.040	0.037	0.003	0.025	0.024	0.001	2.43	0.070	
UP2BL	0.074	0.070	0.004	0.032	0.032	0.000	5.06	0.004	**
UM1MD	0.039	0.037	0.002	0.042	0.041	0.001	1.24	0.404	
UM1BL	0.040	0.037	0.003	0.030	0.029	0.001	1.61	0.207	
LP2MD	0.038	0.036	0.002	0.024	0.024	0.001	2.20	0.095	
LP2BL	0.037	0.034	0.003	0.031	0.030	0.001	1.34	0.300	
LM1MD	0.034	0.032	0.002	0.039	0.038	0.001	1.39	0.341	
LM1BL	0.066	0.062	0.004	0.023	0.023	0.001	7.53	0.001	**

The assumption that variables were normally distributed for both immigrants and locals was examined using the Kolmogorov-Smirnov test ($\alpha = 0.05$) after standardization by Q-mode correction. The greater standard deviation is identified in bold. SD, standard deviation; Boot, bootstrapped standard deviation; Bias, estimated bias for uncorrected standard deviation. Significance level, *, 5%; **,

Table 5. Univariate variance tests for Inariyama population

Variable	Immigrant (n = 3)			Local (n = 9)			F-value	P-value	
	SD	Boot	Bias	SD	Boot	Bias			
UP2MD	0.038	0.031	0.007	0.010	0.010	0.001	10.40	0.006	**
UP2BL	0.036	0.029	0.007	0.020	0.018	0.001	2.52	0.141	
UM1MD	0.027	0.022	0.005	0.034	0.032	0.003	2.06	0.368	
UM1BL	0.050	0.041	0.009	0.023	0.021	0.002	3.70	0.073	
LP2MD	0.044	0.036	0.008	0.017	0.016	0.001	4.88	0.041	*
LP2BL	0.017	0.014	0.003	0.020	0.018	0.002	1.76	0.412	
LM1MD	0.052	0.042	0.009	0.009	0.008	0.001	25.11	0.000	***
LM1BL	0.038	0.031	0.007	0.028	0.026	0.002	1.39	0.303	

The assumption that variables were normally distributed for both immigrants and locals was examined using the Kolmogorov-Smirnov test ($\alpha = 0.05$) after standardization by Q-mode correction. The greater standard deviation is identified in bold. SD, standard deviation; Boot, bootstrapped standard deviation; Bias, estimated bias for uncorrected standard deviation. Significance level. *, 5%; **, 1%; ***,

Table 6. Determinant ratios and randomization *P*-values

Population	$C_{\text{Immigrant}}$	/	C_{Local}	Randomization <i>P</i> -value
Yoshigo	4.77			0.012*
Inariyama	172.95			0.005**

Significance level, *, 5%; **, 1%; ***, 0.1%.